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The Significance of the Permanent Wilting Percentage in Studies of Plant and Soil Water Relations R. O. Slatyer 585

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# THE SIGNIFICANCE OF THE PERMANENT WILTING PERCENTAGE IN STUDIES OF PLANT AND SOIL WATER RELATIONS

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## I. INTRODUCTION

In 1859 Sachs concluded that the amount of water which remains in soil at the time of permanent wilting of plants varies considerably with the type of soil, increasing from sands to clays. Subsequent investigators (Heinrich, 1894; Gain, 1895; Hedgecock, 1902) confirmed his observation and also found that the percentage of water in any one soil when wilting first occurs varies considerably for different species, increasing from hydrophytes to xerophytes, and is influenced by the climatic conditions obtaining at the time of the determination. Cameron and Gallagher (1908) criticised these conclusions, particularly those of Heinrich, on the basis that the permanence of wilting in their experiments was not properly established at the time soil sampling occurred. It was not until the extensive and thorough investigations of Briggs and Shantz (1911a, 1911b, 1912a, 1912b, 1912c), however, that it was demonstrated that the soil water content at the time of permanent wilting shows little variation from plant to plant on any one soil, regardless of the type or age of the plant, or the climatic conditions under which a determination is conducted.

Briggs and Shantz considered this soil value to be highly significant in terms of plant response, as it appeared not only applicable to all plants but also closely associated with the point at which vegetative growth ceases. Their conclusions were supported by the investigations of Capalungan and Murphy (1930) and by the extensive studies of Veihmeyer and Hendrickson (1927, 1928, 1934, 1949) and Hendrikson and Veihmeyer (1929, 1945); and

the permanent wilting percentage, as it was termed by Hendrickson and Veihmeyer (1929), came into widespread use as a soil characteristic, indicating the lower limit of water availability for all plants.

Studies which have determined the physical condition of soil water at the stage of permanent wilting have shown that for most plants the permanent wilting percentage corresponds to a total soil moisture stress value of 10-20 atm. with a mean value of approximately 15 atm. (Thomas, 1921; Edlefsen, 1934; Schofield and da Costa, 1935; Bouyoucos, 1936; Bodman and Day, 1943; Anderson and Edlefsen, 1942; Richards and Weaver, 1943, 1944; Robertson and Kohnke, 1946). This association of physical soil data with permanent wilting has provided further support for the concept of the permanent wilting percentage as a soil constant and has led to still wider application of permanent wilting percentage data.

Although the evidence supporting the concept of the permanent wilting percentage as a soil characteristic appears to be well founded, from time to time the validity of this viewpoint has been questioned from both general and specific points of view. Powers (1922) held that laboratory determinations fail to take account of the variation between plants in the field, and so have limited applicability to natural conditions. Crump (1913) considered that age of plant is important and that the use of seedling plants reduces the significance of results. Other workers have shown that the environmental conditions under which determinations are made are of importance (Brown, 1912; Caldwell, 1913; Shive and Livingston, 1914) and that the permanent wilting percentage can vary with different types of plants (Koketsu, 1928; Swezey, 1942; Fowells and Kirk, 1945; Lane and McComb, 1948; Slatyer, 1957a).

The present review seeks to examine the theoretical basis of the permanent wilting percentage, the factors which influence it, the probable extent of their influence, and the significance of the permanent wilting percentage in studies of plant and soil water relations.

## II. TERMINOLOGY AND PROCEDURE

The term "wilting coefficient" was defined by Briggs and Shantz (1911a, 1912a) as "the water content of the soil at the

time when the leaves of the plant under study first undergo permanent reduction in their water content as a result of a deficiency in the soil water supply. By a permanent reduction is meant a degree of wilting from which the leaves could not recover in an approximately saturated atmosphere unless water was added to the soil." Briggs and Shantz believed that the significance of the wilting coefficient is that it approximately represents cessation of vegetative growth, that it is a constant value for any soil regardless of the plant being studied or the atmospheric conditions under which the study is conducted, and that it is closely related to other soil moisture constants and can be indirectly obtained from them.

Despite the thorough and extensive nature of their investigations, Briggs and Shantz did not provide detailed descriptions of their actual experimental procedure in determining when permanent wilting occurred. They did, however (1912a), state that: "As soon as the plants in a pot have been reduced to a wilted condition from which they can not recover in a damp chamber, the water content of the soil is determined." This was elaborated later by the statement: "A wilted condition in the early morning is considered the best proof that the moisture content has been reduced to the true wilting point. Check determinations were repeatedly made by placing the pots containing wilted plants under a bell jar in nearly saturated air." Failure to recover turgor was regarded as evidence that the wilting coefficient had been reached.

Hendrickson and Veihmeyer (1929) suggested that the term "wilting coefficient" be replaced because their earlier studies (Veihmeyer and Hendrickson, 1927) had shown that the wilting coefficient did not bear a constant relation to other soil constants, as Briggs and Shantz had thought. They proposed the term "permanent wilting percentage" to describe the residual soil water content at permanent wilting, and this term has now been accepted into common usage. Most of their studies (Veihmeyer and Hendrickson, 1927, 1928, 1934, 1949; Hendrickson and Veihmeyer, 1929, 1945) were concerned with field conditions, although they also paid a great deal of attention to determinations of the permanent wilting percentage in containers. They thought that direct determination of the permanent wilting percentage could be made by either of two general methods. The first method was by a system of regular soil sampling during the season, the point at which mois-

ture extraction virtually ceased at any one horizon being taken as the permanent wilting percentage. The second method was by growing and wilting indicator plants in cans in the greenhouse. The plants used for the determination were placed outdoors until wilting became pronounced, when they were transferred to a dark humid chamber for recovery. If recovery occurred, they were replaced outdoors until wilting was again evident, and this procedure was repeated until the plants remained wilted even after 24 hours in the humid chamber. In their field determinations these authors usually worked with well established orchard trees which extracted water fairly uniformly from the wetted part of the soil. Thus the field determination was made either for the whole profile or for each horizon as the moisture extraction curves flattened out. Hendrickson and Veihmeyer (1929) also suggested that the wilted appearance of a plant in early morning can be regarded as an approximate indication of the permanent wilting percentage, although for both field methods they used the laboratory test as their comparative standard. Their findings concurred with those of Briggs and Shantz, although they were more interested in availability of water for transpiration than for growth. They maintained that transpiration is unaffected until the permanent wilting percentage is reached, when it virtually ceases, and that reductions in growth rate do not commence until this point. There are serious objections to the use of field sampling as a method of determining the permanent wilting percentage; these will be considered in a later section.

The next development in terminology was made by Taylor, Blaney and McLaughlin (1934). These workers introduced the concept of a "wilting range" which was defined as the range in water content between the wilting coefficient of Briggs and Shantz and the ultimate wilting point, which was the soil moisture content at which all leaves remain wilted in a humid atmosphere. Furr and Reeve (1945) slightly modified this scheme, introducing the terms "first permanent wilting percentage" (for wilting of basal leaves and cessation of elongation growth) and "ultimate permanent wilting percentage" (for wilting of all leaves). The experimental techniques used by Furr and Reeve are of interest in that they have now been generally adopted in permanent wilting percentage determinations. These workers used sunflowers as their test plants and allowed the plants to grow under conditions

of high water until they reached a satisfactory stage of development. Watering was then discontinued and the plants left in full sunlight until temporary wilting of the basal leaves. They were then moved under a cloth shelter where temporary recovery usually took place. When wilting of the basal leaves recommenced, the plants were moved to a dark humid chamber and left until they recovered. They were then set out once more under the cloth shelter, and this sequence of movements between cloth shelter and humid chamber continued until finally recovery of the basal leaves did not occur in the humid chamber, even after an overnight period. In general, the authors found that the first permanent wilting percentage obtained in this manner corresponded closely with cessation of stem elongation, and they considered that this could be used as an alternate index. Determination of the ultimate permanent wilting percentage was conducted on separate plants in a similar manner. In this case the plants were left under the cloth shelter until all leaves, including the apical ones, were severely wilted before being placed in the chamber. Because of the severe stress through the whole plant system there was never more than slight recovery evident by the apical leaves at this stage and no recovery by the other leaves, most of which were dead.

During the course of time, and largely through the example of Veihmeyer and Hendrickson, the sunflower plant has become the test plant for most determinations. Even so, Briggs and Shantz, and Veihmeyer and Hendrickson have always argued that the permanent wilting percentage does not vary for any one soil, regardless of the plant concerned or the environmental conditions under which a determination is conducted.

## III. THEORETICAL CONSIDERATIONS

In order to understand the factors which influence the permanent wilting percentage, it is of value to examine the sequence of events which occurs in plant and soil as a plant dries the soil from field capacity.

In Figure 1, a diagrammatic representation of this situation is depicted. This envisages very thorough root exploitation of the soil so that it represents conditions as obtaining in a can instead of a field. For the sake of simplicity, it is also assumed that the

osmotic characteristics of all tissues of the plant are similar, and that classical osmotic theory is valid.

Two simple but necessary points are at once evident. The first is that there is a progressive increase in total soil moisture stress (TSMS)[1] each day as a result of soil water depletion. In the diagram TSMS represents the soil water conditions at the root surfaces, so that during each day there is an increase in TSMS, and during each night recovery tends to occur as soil water moves from the soil mass to the root surface. The second point is that the diffusion pressure deficit (DPD)[2] of the water in a plant is never lower than the TSMS unless water is being absorbed directly from the atmosphere by the top of the plant. This is theoretically essential if water is not to move back from the plant into the soil.

An examination of Figure 1 shows that on day O, TSMS is at a value of 1-2 atm., even when the soil is at saturation. A value of this magnitude may occur in fertilised cultivated soils due to the effects of osmotically active substances in the soil solution. As water depletion occurs each day, TSMS and DPD increase progressively, with the gradient from soil to plant becoming less steep, and recovery in both TSMS and DPD becoming slower each night until, as indicated on the final day, recovery of DPD does not proceed at a sufficient rate to enable DPD-TSMS equilibrium by sunrise.

Each morning, with the progessive increase in DPD, there is an associated decrease in turgor pressure, as recovery in turgor each night is limited by the degree to which recovery in DPD can proceed. At first this decrease of turgor is not visible, but as it becomes more pronounced with the progressive fall in turgor pressure, the leaves gradually take on a more and more wilted appearance.

In applying this to a consideration of the permanent wilting percentage, it must be remembered that permanent wilting is represented by a completely wilted appearance of a specified part of the plant, usually the active leaves. It seems logical to expect

[1] Total soil moisture stress (Richards and Wadleigh, 1952) represents the diffusion pressure deficit of the soil water, being equivalent to the combined effect of the soil moisture tension and the osmotic concentration of the soil solution.

[2] Using the terminology of Meyer (1945).

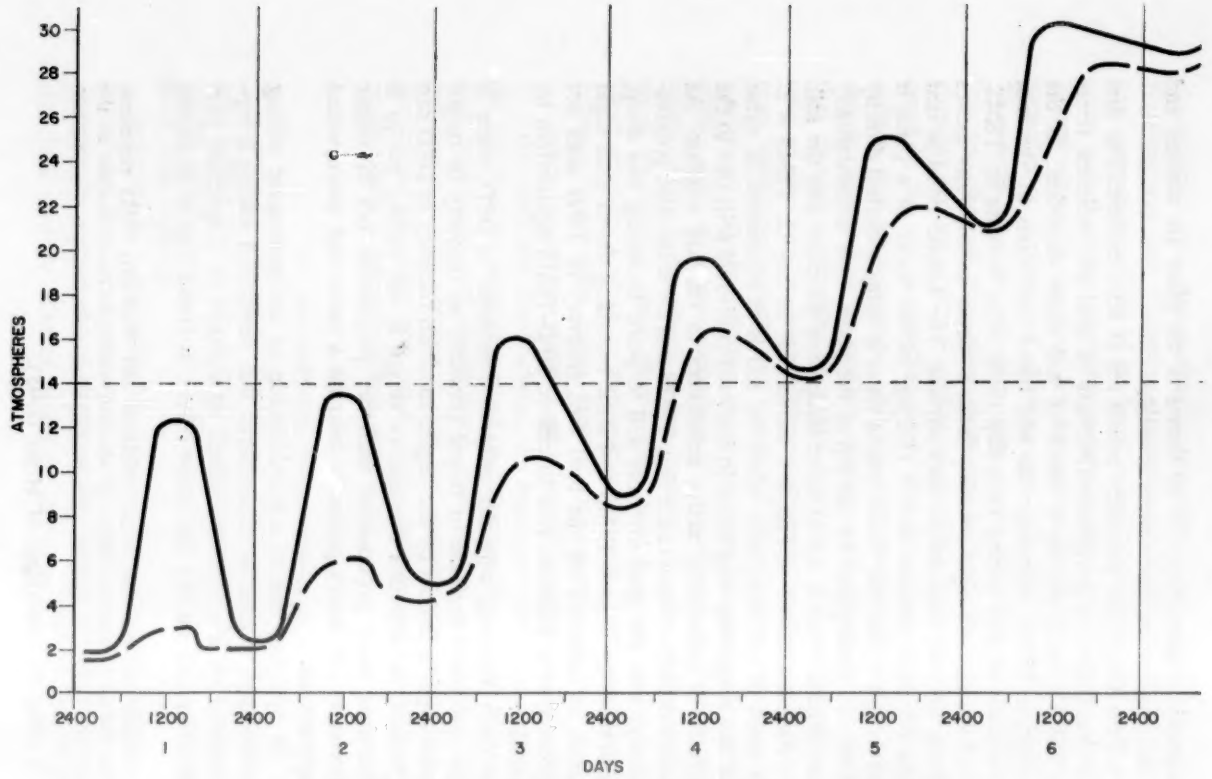


Fig. 1. Diagrammatic representation of diurnal changes in DPD (continuous line) and TSMS (broken line) as soil is dried progressively from field capacity.

that in plants which respond sensitively to changes in turgor, such as mesophytes, the development of DPD in a leaf, such that the average DPD is equal to the average osmotic pressure, would cause the average turgor pressure to be effectively reduced to zero and the appearance of complete wilting to develop. It is also probable that, with decreasing turgor, growth and other plant functions will progressively decrease to cease at a DPD approximately equivalent to the stage of zero turgor pressure. These assumptions have been generally borne out by experimentation (Herrick, 1933; Furr and Reeve, 1945; Slatyer, 1957a). With xerophytes and plants with rigid leaves the appearance of wilting may not develop until greater DPDs exist than those at zero turgor pressure, but the significance of this point with respect to plant function will remain (Slatyer, 1957a).

If these assumptions are valid it would appear that this stage of zero turgor pressure is the fundamental point of permanent wilting. This means that the permanent wilting percentage would be the soil water content which exists when there is DPD-TSMS equilibrium, and zero turgor pressure in the indicator tissue of the plant. This can be interpreted in Figure 1 if a horizontal line is drawn at, say, a level of 14 atm., representing the osmotic pressure of the leaf tissue when the average turgor pressure has fallen to zero. Each day, as the soil dries out, there is a progressive increase in TSMS and DPD, and an associated decrease in turgor. This process continues until, even after nocturnal recovery has proceeded to DPD-TSMS equilibrium, the DPD is at a level equal to the arbitrary 14-atm. level, when the plant can no longer regain turgor to the extent that there will be any positive turgor pressure, and wilting will become permanent unless the TSMS is reduced by addition of water to the soil.

In an actual determination of the permanent wilting percentage (Furr and Reeve, 1945) the plants are placed in a humid atmosphere as soon as diurnal wilting becomes evident (as for example in Figure 1, on day 3, when the DPD exceeds the zero turgor pressure line at midday). Upon recovery the plants are set out in a shaded area; wilting and recovery then proceed intermittently until the permanent wilting percentage is reached. Recovery of DPD in a humid chamber would be more rapid than recovery as shown in Figure 1, and rate of increase in TSMS would possibly

be slower due to reduced rates of soil water depletion. Fundamentally, however, the point at which permanent wilting would occur would still be equivalent to zero turgor pressure in the plant tissues, so that the permanent wilting percentage would be at a TSMS equivalent to the DPD at this value.

The principal point which emerges from this analysis is that the permanent wilting percentage is fundamentally a value determined not by any soil characteristics but by the osmotic characteristics of the plant. In particular the osmotic concentration of the cell sap is important because it is this value which determines the DPD that exists at zero turgor pressure in the cells of the indicator tissue.

Theoretically, the factors which will influence the permanent wilting percentage will be those which affect the osmotic pressure of the tissue fluids. In practice, however, the theoretical model is not always reproduced, and this is particularly true of a field determination of the permanent wilting percentage. Therefore, additional important factors are those which affect the attainment and recognition of DPD-TSMS equilibrium at the stage of zero turgor pressure. These include factors which influence the TSMS at the root surface and those which determine whether or not the TSMS at the root surface is representative of the value for the soil mass, together with experimental factors associated with the reproducibility of the determinations.

## IV. SIGNIFICANCE OF WILTING PHENOMENA IN PLANTS

There is now general agreement that the availability of soil water for plant growth decreases progressively as soil moisture stress increases (Richards and Wadleigh, 1952) and that the first evidence of decreased growth occurs at quite low stress levels. Evidence to the contrary (Veihmeyer and Hendrickson, 1950) is based mostly on field experimentation, the proper interpretation of which is rendered difficult because of the variation which exists between different experiments with respect to root distribution, total depth of the root zone, and other experimental factors.

Most of the experiments relating water stress to growth have been conducted either with different watering regimes, which allowed depletion of soil water to different degrees before rewatering, or with osmotic substrates which simulated various degrees of

TSMS. In the former type of study, decreases in growth and dry matter production were normally found in the first treatment which allowed significant depletion of soil water below field capacity (Davis, 1942; Scofield, 1945; Gates, 1955a, 1955b). In some instances reductions in growth and yield have been observed at soil moisture tensions as low as 0.7 atm. (Haynes, 1948; Salter, 1954). The results from experiments which have simulated degrees of TSMS by using culture solutions of known osmotic pressure, or by adding osmotically active substances to soils, have given similar results. With a wide variety of crops, growth was impeded at low soil moisture stress values, and the degree of inhibition increased progressively as TSMS increased (Hayward and Long, 1943; Ayers, Wadleigh and Magistad, 1943; Wadleigh and Ayers, 1945; Wadleigh, Gauch and Magistad, 1946; Bernstein and Pearson, 1954).

These reductions in growth are caused primarily by decreasing hydration in the plants. It is sometimes suggested that because the slope of the water absorption gradient from soil to plant remains the same as stress increases, there is no change in the availability of water to the plant and so growth should not be affected. This argument, although it may apply, with reservations, to aspects of transpiration, is not applicable to growth. As the DPD in the plant can never fall to a level lower than the TSMS, with increasing stress there is essentially decreasing turgor in the plant tissues, and this is reflected in a progressive decrease in growth. It is to be expected that growth should cease at or before a DPD exists such that there is zero turgor in most of the plant tissues; this is indicated by the studies which bear directly on this point (Wadleigh and Ayers, 1945; Wadleigh, Gauch and Magistad, 1946; Slatyer, 1957a) as well as by indirect evidence from experiments concerned with the effects of water stress on elongation and photosynthesis.

The effects of water stress on elongation generally act directly through the effect of turgor pressure on cell enlargement. Such an effect can be induced by the general level of tissue hydration in the plant or by the additional effect of a diurnal water deficit induced by transpiration. Thus stem elongation can be completely inhibited by bright sunlight, even when the soil water level is high (Balls, 1912; Loomis, 1934), but, in general, rate of elongation

decreases as the soil dries from field capacity, to cease at a TSMS approximating to the permanent wilting percentage (Furr and Reeve, 1945; Wadleigh and Gauch, 1948; Blair, Richards and Campbell, 1950; Clements, Shigeura and Akamine, 1952). On occasions, stem elongation has been observed at DPDs so high that the plant as a whole was losing weight (Wilson, 1948; Slatyer 1957a); this probably suggests that forces other than simple osmotic elements are involved, such as those suggested by Kerr and Anderson (1944).

Photosynthesis is affected by water stress, directly as a result of tissue hydration and indirectly as a result of stomatal closure and its influence on gas exchange. Rabinowitch (1945) reported results by various workers which showed that low leaf water content in itself could affect photosynthesis. Walter (1929) demonstrated that with water plants in solutions of different osmotic pressure, there was a direct relationship between cell turgor and rate of photosynthesis. In general, reductions in photosynthesis commence at low DPD values and increase progressively until photosynthesis ceases at a DPD fairly close to zero turgor pressure but dependent on the plant and tissue involved (Schneider and Childers, 1941; Loustalot, 1945; Bordeau, 1954). This is probably largely a function of the indirect effect of stomatal closure on photosynthesis. Yocum (1935) found that stomatal closure in oak seedlings caused complete disappearance of starch from the leaves, and Nutman (1937) with coffee observed that midday closure of stomates caused a marked decrease in photosynthesis. On the other hand, Mitchell (1936) found that tomato and pelargonium plants continued to absorb $CO_2$ when the stomates appeared closed. In leaves in which the cuticle is permeable to gases, it would seem that gas exchange may continue after stomatal closure, as Freeland (1948) suggested, and so photosynthesis could occur even when the stress is such that the stomates are completely closed all day.

These results suggest that the onset of permanent wilting, associated as it is with reduction of the general levels of turgor pressure to zero, is a significant indication of cessation of vegetative growth. Although variation can be expected from plant to plant, and tissue to tissue, it is apparent that when such processes as cell enlargement and photosynthesis have ceased in the leaves, there will be virtually no further vegetative growth in the plant as a whole.

The effect of decreasing turgor on transpiration is not so direct as on essentially physiological functions such as growth. Transpiration is basically a passive process and as such is determined largely by the diffusion gradient from leaf to atmosphere and the rate of water supply to the roots. The effect of leaf water content in itself is not likely to affect transpiration unless severe wilting occurs (Gregory, Milthorpe, Pearse and Spencer, 1950). The main regulating influence of the plant lies in the effectiveness of stomatal closure in restricting transpiration. In turn, this effect depends on the degree of cuticular transpiration and on the sensitivity of stomatal movement to changes in turgor. In most xeromorphic plants cuticular transpiration is very slow, but in many mesophytic species considerable quantities of water can be lost even if the stomates are closed. Magness, Degman and Furr (1935) considered stomatal closure to be the most sensitive index of water deficits in apple trees and that stomatal closure occurs at soil moisture stress values of only a few atmospheres. Oppenheimer and Elze (1941), working on citrus trees, also regarded stomatal movement as sensitive to small changes in leaf water content. Any factor causing loss of turgor will tend to cause stomatal closure, and with rapid transpiration stomatal closure is frequently observed (Oppenheimer and Mendel, 1939), even when TSMS is at a value close to field capacity.

The effect of water stress on transpiration will also depend on the evaporating conditions. A plant-soil system which is capable of absorbing and transpiring water at a rapid rate under arid atmospheric conditions would not be expected to show reduced transpiration under mild evaporating conditions until TSMS reaches a high enough level to reduce total absorption below the transpiration requirement. If conditions favor rapid evaporation, however, water deficits quickly develop in the plant system and stomatal closure would be expected to limit transpiration, probably in conjunction with limitations in supply occasioned by inadequate flow to the soil-root inter-surface.

For reasons such as those given above, and also because of the conflicting and complicated evidence from field experiments, there is a good deal of controversy about the effects of water stress on transpiration.

Veihmeyer and Hendrickson (1955) have claimed that tran-

spiration is unaffected by TSMS until the permanent wilting percentage is reached. Similar results have been obtained by other workers (Furr and Taylor, 1939; Wadsworth, 1934), but most studies have indicated that reductions in transpiration rate commence at much lower tensions (Chung, 1935; Martin, 1940; Slatyer, 1956a; Bloodworth, Page and Cowley, 1956). Since some reduction in transpiration rate must occur in conjunction with stomatal closure, it would seem that initial reductions in rate would be observed at stress values well below those at permanent wilting. The results of Veihmeyer and Hendrickson appear to be explicable on the basis that, as suggested above, the absorption capacity of the plant roots exceeded the transpiration rate until the TSMS rose high enough to restrict absorption, or that in the field experiments, which provided most of the supporting evidence, enough of the root system was in soil zones of low TSMS to maintain the general turgescence of the plant at a high level until the upper soil horizons were dried to a point close to the permanent wilting percentage.

Veihmeyer and Hendrickson (1927, 1934, 1949, 1950) and Hendrickson and Veihmeyer (1929, 1945) have also claimed that under field conditions absorption from any soil zone ceases when the soil water content is reduced to the permanent wilting percentage. There seems no valid reason why this should occur, and results from other field studies (Batchelor and Reed, 1923; Taylor and Furr, 1937; Swezey, 1942; Haise, Haas and Jensen, 1955) and from almost all laboratory experiments (Briggs and Shantz, 1912a; Hendrickson and Veihmeyer, 1945; Slatyer, 1957a) demonstrate continued absorption beyond the permanent wilting percentage, extending sometimes after death of the plant. As Veihmeyer and Hendrickson's field determinations were generally confined to the top few feet of soil, and the lower limit of the soil water reservoir or of root penetration was not stated, it would seem that the reason for the apparent cessation of water extraction at the permanent wilting percentage would be that differential absorption occurred from different soil horizons. At first, water extraction would be expected to proceed rapidly in the zones of highest root intensity (Aldrich, Work and Lewis, 1935; Veihmeyer and Hendrickson, 1938), but as the TSMS rose in these zones, more water would be absorbed from other horizons

where it was still at lower tensions (Hayward and Spurr, 1943). Under these conditions the DPD in the conducting system of the plant would probably be of the order of 5-10 atm. (Renner, 1911; Stocking, 1945) so that when the TSMS in the upper soil horizons reached a value of this magnitude, absorption from these horizons would virtually cease, and further reductions in soil water content would possibly not be measurable. The value at which this occurred would appear very close to the permanent wilting percentage when interpreted on the basis of soil water content.

To sum up, it may be expected that the influence of soil moisture stress on transpiration will vary considerably from plant to plant, depending on evaporating conditions, on effectiveness and sensitivity of stomatal closure, and on the availability of water for absorption (dependent in turn upon the extent of the root system, on rate of flow of soil water to the root surface, on TSMS at the root surface and on the rate of root growth into the soil mass). In general, resistance to the passage of water into and through plants, by reduced permeability of the roots (Kramer, 1950) and other factors, is small compared to the resistance at the leaf-air surface (Gradmann, 1928; van den Honert, 1948).

Instead of ceasing at any particular stress level, transpiration would appear to be limited by the above considerations and to vary from plant to plant and with environmental conditions. The influence of permanent wilting on transpiration and absorption would therefore seem to be indirect and not nearly so significant as the relationship with active plant processes such as growth.

## V. FACTORS AFFECTING THE PERMANENT WILTING PERCENTAGE

The permanent wilting percentage is determined as soil water content at the time when the leaves of the plant under study have reached a degree of wilting from which they will not recover in a humid atmosphere. This corresponds to a point of equilibrium between the DPD in the plant and the TSMS of the soil water, at a DPD such that there is zero turgor pressure in the indicator tissue. The factors which affect the permanent wilting percentage are those which affect the TSMS/water content characteristics of any one soil; those which affect the uniformity of the TSMS in the soil mass, and hence determine whether or not the TSMS at the root surface is typical for that of the soil mass; those which in-

fluence the attainment of DPD-TSMS equilibrium; and those which influence the DPD at which there is zero turgor in the indicator tissue.

### Relationship Between Water Content and TSMS in Soils

As the permanent wilting percentage is measured in terms of soil water content, the primary factor causing variation in the value obtained is the soil water characteristic curve, which relates soil water content to TSMS for any one soil. In this discussion, however, it will be assumed that readers are familiar with the general energy concepts of soil water relationships (Kramer, 1949; Richards and Wadleigh, 1952) and that the dynamic aspect of soil water with respect to the permanent wilting percentage is not soil water content but TSMS.

Thus, although considerable variation in soil water content exists between soils at any one TSMS, depending on the water retention characteristics of the soil and the osmotic characteristics of the soil solution, the permanent wilting percentage, if a valid soil constant, should occur at constant TSMS regardless of soil type.

Some change in TSMS at any one water content, with respect to temperature, will occur, but within the range of temperatures normally encountered by growing plants the effect can be expected to be slight (Richards and Weaver, 1944). These authors showed that there was a negative effect of temperature on soil water retention at any one moisture content, due primarily to the influence of temperature on surface tension. The change in water retention per degree change of temperature increased from coarse to fine textured soils. The order of change at 15 atm. tension in some of the finer textured soils tested was two per cent per 10 °C change in temperature, but in the coarser soils was seldom more than half of this amount. At 0.5 atm. tension there was negligible change. The effect of temperature on the osmotic component of TSMS, being a function of absolute temperature, should likewise not be of significance within the normal range of temperatures and salt concentrations encountered, although it could be important in saline soils.

### Factors Affecting the Uniformity of TSMS in the Soil Mass

In the theoretical model described in Figure 1, it was assumed that rate of water movement in the soil was adequate to virtually

eliminate gradients in TSMS through the soil mass by sunrise each day. In practice this is not necessarily the case, and it is probable that cumulative effects can cause the development of wide differences between the TSMS at the root surface and in the soil mass.

The primary factor causing the development of differences in TSMS is the rate of water extraction by the plant relative to the rate of supply. This depends on transpiration rate and rate of water movement to the roots. The latter factor is detemined not only by rate of flow but also by the distance which water has to move, and so is influenced considerably by root density and root growth.

Although unsaturated flow is slow in soils drier than field capacity (Richards and Wadleigh, 1952), evidence from pressure membrane experiments (Richards and Weaver, 1944) indicates that rates of flow under fairly small pressure differences are high enough to enable water to move several millimeters in a few hours. This would suggest that under conditions of high root density, as found with established plants in containers, water movement would be fast enough to eliminate most gradients in TSMS during the overnight period of slow transpiration.

Indirect evidence on the relative importance of unsaturated flow in influencing the TSMS at the root surface, with plants grown in containers, is available from experiments which have studied the influence on growth of plants of different degrees and combinations of soil moisture tension and osmotic pressure (Ayers, Wadleigh and Magistad, 1943; Wadleigh and Ayers, 1945; Wadleigh, Gauch and Magistad, 1946). These investigations demonstrated that with increasing TSMS similar reductions in plant growth were caused regardless of whether the TSMS was composed mainly of osmotic pressure or mainly of soil moisture tension. Thus, in treatments in which the TSMS was made up almost entirely of soil moisture tension, and in which unsaturated flow could be expected to have been of importance in determining the availability of water, no difference in growth was found compared to treatments in which the TSMS was almost entirely of osmotic origin, and in which unsaturated flow would have been of no consequence. Richards and Weaver (1944) found with 24 soils, ranging from sands to clays, and with varying degree of salinity, that there was no significant difference in the TSMS at permanent wilting of sunflowers as determined by Furr and Reeve (1945). These plants were also

grown in small containers, and again it would seem that the different unsaturated flow characteristics of the different soils were not important in influencing the uniformity of TSMS in the soil mass.

These results suggest that as long as root density is high, as is the case with plants grown in containers, water movement in the soil overnight is adequate to make the TSMS substantially uniform through the soil mass. Under field conditions, root density can be much lower and considerable gradients in TSMS through the soil mass can be expected to develop, depending on the root density in any one soil zone. The water extraction picture under field conditions, which reflects most rapid extraction in zones of highest root density, is evidence of this (Aldrich, Work and Lewis, 1935; Russell, Davis and Blair, 1940; Doneen, 1942; Kelley, 1954; Corey and Blake, 1953; Russell and Danielson, 1956).

Root extension into moist soil provides an alternative agency whereby in field soils of sparse root distribution, more soil water can come into contact with the absorbing surfaces of the roots (Dittmer, 1937; Kramer and Coile, 1940). Root extension can be expected to cease when increasing DPD reduces the turgor pressure in the elongating root tissue to zero, or when critical high or low temperatures for any particular species occur (Kramer, 1940). The former factor could partially explain why in field soils some observers have found that water extraction appears to cease in any one horizon at about the permanent wilting percentage because, if root distribution is relatively sparse, root extension could be a more important agency for water absorption than soil water movement. This would be particularly true if unfavorable soil temperatures were to accentuate the effects of high TSMS on root growth.

The effects of temperature gradients in the soil have a direct influence on the rate of unsaturated water flow and on vapor movement. The latter effect is of particular importance where temperature gradients could result in transport of water towards cooler parts of the soil and its subsequent condensation, thus reducing the TSMS of the soil water in the condensing area. This could occur in the field, in response to diurnal temperature fluctuations, and also in the laboratory, if the containers used for permanent wilting percentage determination were exposed to direct sunlight and the layers of soil adjacent to the walls became heated.

### Factors Affecting the Attainment of DPD-TSMS Equilibrium

Since factors which influence the uniformity of TSMS in the soil mass were considered above, this section will deal primarily with the attainment of equilibrium between the DPD in the plant and the TSMS at the root surface.

Rate of water movement from the soil mass to the roots is the primary factor which limits recovery in DPD by the plant on any one day. It is accentuated by the factors of root density and root elongation, which determine the distance the water has to move and so influence the total amount of water available for absorption. It is also affected by the transpiration rate, which determines the extent of the water deficit in the plant and hence the amount of water needed to reduce the DPD to the point of DPD-TSMS equilibrium.

Theoretically, transpiration rate should have no influence on DPD-TSMS equilibrium as long as a sufficient recovery period is available for the establishment of equilibrium conditions. In practice, however, it can have an effect even in laboratory determinations of the permanent wilting percentage.

If atmospheric conditions are mild and favour slow transpiration, DPD-TSMS equilibrium should be established by sunrise each morning, even in field soils with sparse root distribution. On the other hand, if conditions exist which favour rapid transpiration, a DPD of 40-50 atm. can be developed in the plant during the day, and even in moist soils rate of recovery of DPD at night may not be fast enough to enable DPD-TSMS equilibrium to be reached by morning. In a laboratory determination plants are withdrawn from outdoor conditions as soon as wilting becomes evident so that permanent wilting is approached slowly, but under field conditions, where rate of approach cannot be controlled, marked variation, depending on the evaporating conditions, can be expected in the TSMS at which early morning wilting occurs. Effects of severe wilting of any tissue can also cause irreversible damage and failure to regain turgor (Furr and Reeve, 1945).

Rapid transpiration can also cause accumulation of salts at the root surface, for increase in solute absorption is not proportional to increase in transpiration rate (Freeland, 1937; Wright, 1937; Hoagland, 1944). This would change the soil water content/TSMS characteristics at the root surface and would prevent attainment

of equilibrium at a value characteristic of that of the soil mass. It would be more significant if shrinkage of soil and root tissue during dehydration caused substantial discontinuities to develop in the soil-root liquid system because such a vapour gap would inhibit further mineral absorption. Such discontinuities could also result in slower absorption, as absorption would be dependent on vapour transport across the soil-root gap, and would cause delayed attainment of DPD-TSMS equilibrium.

In laboratory experiments, an important procedure to assist in attaining DPD-TSMS equilibrium is to place the plants in a humid chamber, so that transpiration virtually ceases and recovery of DPD and elimination of TSMS gradients in the soil can proceed unimpeded by further water losses from the plant. The degree of recovery in the humid chamber will depend very much on the vapour pressure of the air in the chamber and on the time available for recovery. If the humidity in the chamber is so high that the DPD of the vapour is lower than the DPD of the plant, there is a high probability that there will be uptake of water from the atmosphere directly by the aerial parts of the plant (Breazeale, McGeorge and Breazeale, 1950, 1951; Haines, 1952, 1953; Breazeale and McGeorge, 1953a, 1953b; Slatyer, 1956b). This could cause temporary reduction in DPD to a level below that of the TSMS. Visual assessment of the degree of wilting might then indicate that permanent wilting had not been reached. If this occurred the plant could continue to deplete the soil water reservoir and hence increase the TSMS above the correct value for DPD-TSMS equilibrium at permanent wilting. Alternatively, if the humid chamber were only at, say, 95-96 per cent relative humidity (equivalent to about 60-70 atm. DPD at 20 °C), slight transpiration may continue and delay the attainment of equilibrium. It could be imagined that under some circumstances the standard overnight or 24-hour period allowed for equilibration could be too short.

The effects of temperature on the attainment of DPD-TSMS equilibrium will be primarily those associated with reduced rates of water movement in soils at low temperatures (described above) and with reduced rates of water absorption at high and low temperatures.

Reduction in rate of absorption with decreasing temperature

depends largely on the species concerned, plants indigenous to warm climates exhibiting a greater degree of reduction than those native to cool climates (Döring, 1935; Brown, 1939; Kramer, 1942). High soil temperatures may also limit absorption (Bialoglowski, 1936; Haas, 1936; Kramer, 1940). In general Kramer (1949) concluded that the primary cause of reduced intake at low temperatures is the physical effect of increased resistance to water movement across the living cells of the roots, due to the continued effects of decreased permeability and increased viscosity of the protoplasm of the root cells, and the increased viscosity of the water being absorbed. The effects of reduced absorption would be of most importance under field conditions, where the absorption lag can be greatest, although the slower onset of temperature changes in the field would enable some degree of adaptation by the plant tissues to occur (Kramer, 1949), and in the field, plants generally adapted to the environment are grown. Under laboratory conditions the period of recovery in the humid chamber would normally seem to be adequate to enable DPD-TSMS equilibrium to be obtained, even with reduced rates of absorption. With sunflowers, Hendrickson and Veihmeyer (1945) observed that the permanent wilting percentage was unaffected by temperature until the soil temperature fell to 5 °C.

### Factors Affecting the DPD at Permanent Wilting

These are the factors which influence the osmotic characteristics of the plants as well as recognition of permanent wilting at the stage of zero turgor pressure.

The important osmotic characteristic is the osmotic pressure of the leaf tissue when the DPD has increased until there is zero turgor pressure. This value is seldom measured directly except in determinations of the osmotic pressure at incipient plasmolysis, but evidence of the extent to which osmotic pressure of the leaves can be expected to vary with respect to species of plant, general habitat, climatic and soil conditions, is available in the extensive literature on this subject.

The osmotic pressure of the cell sap varies markedly with different ecological groups of plants and with plants from different environments (Iljin, 1929; Walter, 1931; Harris, 1934). Within any one group variation also occurs with type of plant, usually

increasing from herbs to shrubs to trees (Harris and Lawrence, 1916). The general levels of osmotic pressure in the leaves of most mesophytic plants range from about 5 to 20 atm. (Meyer, 1956; Stocking, 1956). In xerophytes and desert plants values of 30-40 atm. are common and values up to 60 atm. have been reported (Maximov, 1929; Evenari and Richter, 1937; Poljakoff, 1945; Oppenheimer, 1950). Values in excess of 100 atm. are usually found only in halophytes (Harris, 1934), and the highest value recorded, 202.5 atm., was obtained for *Atriplex confertifolia* in its natural habitat by Harris (1934).

It is evident that differences in osmotic pressure of this magnitude can have a marked effect on the DPD and hence the TSMS at which permanent wilting occurs, and so can significantly shift the permanent wilting percentage, expressed as soil water content, even in coarse textured soils.

These general levels of osmotic pressure are characteristic of the various plant types in their natural habitats. Marked variation in osmotic pressure occurs, regardless of species, with respect to diurnal and seasonal influences and with any other environmental changes.

Diurnal changes in osmotic pressure are caused by changing water content, hence changing cell sap concentration, as a result of the lag of absorption behind transpiration, and by accumulation of soluble carbohydrates as a result of photosynthesis. Both of these effects tend to cause an afternoon maximum and pre-dawn minimum in osmotic pressure, with a possible diurnal range of 5-10 atm. (Herrick, 1933; Stoddart, 1935).

Seasonal conditions are of influence primarily through associated effects of water stress on osmotic pressure. These effects can be direct, resulting from reduced water content causing an increase in cell sap concentration (as above), or indirect, resulting from accumulation of salts from the soil solution (Harris, Gortner, Hoffman, Lawrence and Valentine, 1924; Stoddart, 1935), or from breakdown or organic complexes to osmotically active substances (Ahrns, 1924; Spoehr and Milner, 1939). The extent of such changes can be gauged from the work of Harris et al (loc. cit.) who found that the leaves of *Atriplex muttallii* had an osmotic pressure of 38 atm. under moist conditions, and of 169 atm. under dry conditions two months later, and of Stoddart (1935)

who noted that the osmotic pressure of upland and prairie species in non-saline soil increased by up to 30 atm. as the soil dried out.

The extent to which adjustments in osmotic pressure can be made depends mainly on the rate of onset of stress (Hibbard and Harrington, 1916) and on the length of the period to which the plant has been subject to stress, particularly if the soluble salt concentration of the soil is high (Hibbard and Harrington, 1916; McCool and Millar, 1917; Stoddard, 1935; Oppenheimer, 1950). With rapid onset of stress little change in osmotic pressure can be expected, and under laboratory conditions Slatyer (1957a) found that, even when onset of wilting took 11 days, a period longer than usual in laboratory determinations of the permanent wilting percentage, the increase in cell sap concentration was almost entirely that to be expected as a direct result of decreased hydration.

With special reference to determinations of the permanent wilting percentage, Veihmeyer (1956) reported that addition of soluble fertilisers, even in very large amounts, was without effect on the permanent wilting percentage. It could be expected that the first effect of adding soluble materials to the soil would be to increase the TSMS at any one soil water content (Thomas, 1939; Wadleigh and Ayers, 1945; Wadleigh, Gauch and Strong, 1947; Ayers and Campbell, 1951), and so depress the soil water content at permanent wilting. After a period of time, however, it is probable that a sufficient amount of the added salts would be absorbed by the plant to raise the osmotic pressure, and hence the DPD at zero turgo pressure, by an amount approximately equivalent to the increase in TSMS (Eaton, 1927). This would mean that, although the TSMS at permanent wilting would be raised considerably, the soil water tension, and soil water content, would remain substantially unchanged and the permanent wilting percentage would be at the same value. The experiment of Henderson (1951) supports this explanation. With plants grown from seed in soils to which different quantities of NaCl had been added, he found that the soil water content at the permanent wilting percentage was unaffected by increasing NaCl, indicating that the increase in the osmotic pressure of the soil solution was balanced by increase in the osmotic pressure of the plant. When the plants were grown in normal soils and then watered with a range of saline solutions, however, the water content at which permanent wilting occurred

increased with increasing concentration of the added solution. In this case the osmotic pressure of the plant apparently did not have time to change significantly, hence the TSMS at the permanent wilting percentage remained the same, but the soil water content increased with increasing quantities of added NaCl.

It is clear from the foregoing not only that variation in osmotic pressure can be expected from plant to plant and between plants from different environments, but also that environmental changes during the life of any one plant can be of considerable importance. Under field conditions considerable variation can be expected in the DPD at which permanent wilting occurs, depending on the extent to which the above factors operate. Under laboratory conditions less variation can be expected because of the more uniform conditions under which the plants are grown, but the question must then be raised as to the validity of determinations which are made under environmental conditions different from those of the natural habitat of the particular species concerned.

Besides effects on the overall osmotic levels of plants, the fact that the osmotic pressure varies in different plant tissues means that the TSMS which is associated with permanent wilting will vary, depending on the tissue used as an indicator. In general there is a gradient of osmotic pressure through a plant from root to top and from lower to upper leaves (Hannig, 1912; Dixon, 1914; Dixon and Atkins, 1916; Miller, 1938; Stocking, 1956), the most active tissues photosynthetically being those with highest osmotic pressures, so that young or exposed leaves generally have higher values than old or shaded leaves( Dixon and Atkins, 1912; Lutman, 1919; Halma and Haas, 1928; Marsh, 1940). In trees, however, Korstian (1924) and Gail and Cone (1929) observed that the oldest leaves had the highest values. Furr and Reeve (1945) found that the osmotic pressure of the lower leaves of sunflowers at permanent wilting was 9 atm. and of the apical leaves was 22 atm. These variations are large enough to introduce errors to permanent wilting percentage determinations unless the actual leaf used to indicate wilting is specified, and it was for this reason that Furr and Reeve introduced their concept of "first" and "ultimate" permanent wilting.

The association of permanent wilting with the point of zero turgor pressure depends on the sensitivity of the leaf responses

to changes in turgor and on observer differences in assessing wilting. Richards, Campbell and Healton (1949) found that the TSMS at permanent wilting of sunflowers and cotton ranged from 7-43 atm., depending on the severity of wilting. In general most mesophytic plants show good agreement between the appearance of permanent wilting and the development of zero turgor pressure (Herrick, 1933; Furr and Reeve, 1945; Slatyer, 1957a). With xeromorphic plants, however, the appearance of wilting may be delayed until much higher DPDs exist (Briggs and Shantz, 1912a; Daubenmire and Charter, 1942; Fowells and Kirk, 1945). In privet, with relatively rigid leaves, Slatyer (1957a) found that by the time wilting was apparent the TSMS was 48 atm., although the DPD at zero turgor pressure was only 27 atm. With some plants with rigid leaf tissue, and particularly with some xeromorphic species, it would seem that difficulties in recognition of wilting could be such as to invalidate determinations unless indirect methods of recognition are developed (Briggs and Shantz, 1912a).

## VI. EXTENT OF ERRORS IN DETERMINATIONS OF THE PERMANENT WILTING PERCENTAGE

The discussion in the preceding chapter demonstrated that the attainment of DPD-TSMS equilibrium at the point of permanent wilting, such that there is uniformity of TSMS in the soil mass and of DPD in the plant, can be difficult to obtain, particularly in field determinations. It also brought forward the point that the DPD (and hence the TSMS) at which permanent wilting occurs can be expected to vary with the plant under study and the experimental conditions. In order to establish whether or not the extent of variation in TSMS at permanent wilting is enough to significantly affect the concept that the soil water content at permanent wilting is a constant, it is necessary to summarise the probable cumulative effects of the various sources of error with respect to field and laboratory determinations.

### Field Determinations

The standard method for determining the permanent wilting percentage under field conditions (Hendrickson and Veihmeyer, 1929, 1945; Veihmeyer and Hendrickson, 1949) is to measure

the soil water content in any one soil horizon, when moisture extraction in that horizon appears to cease.

Differences in the soil water content at this point are caused primarily by the distance water has to move to the roots, which is a function of rate of water movement in unsaturated soils and of root growth and root density. The total amount of water in the soil profile and the slope of the absorption gradient from root to soil, in relation to root distribution, are also of importance.

As an extreme example of the possible difference in the point at which extraction ceases, a comparison may be drawn between a young plant with sparse root distribution in a field soil, and a well established plant with very high root density in a small container. In the former case much of the water in the soil mass would remain virtually untapped because of the distance water would have to move to the roots. When the TSMS at the root surface became high enough to inhibit root growth, extraction would probably appear to cease, yet the TSMS in the soil mass would be only of the order of a few atmospheres. In the latter case extraction may continue at a significant rate to a point beyond the death of the plant, when the TSMS may exceed 100 atm. (Slatyer, 1957a). In general, however, no such extreme situations arise under normal field conditions. More normal situations are those in which there is soil water available below the normal root depth and where there is a marked decrease in root density with depth, or in which the soil is wetted only to a few feet and density is moderate to high throughout.

If water is available at depth in the soil, most of the water extracted from the soil in the first few days after rainfall or irrigation is removed from the surface layers where root density is highest (Weaver, 1926; Weaver and Bruner, 1929; Coile, 1937; Billings, 1938). As the TSMS in these layers increases, however, and the DPD gradient favouring water movement from soil to root is reduced, the proportion of water absorbed from them will be reduced (Eaton, 1942; Hayward and Spurr, 1943) and the proportion of water absorbed from deeper horizons, where water is still available at low TSMS, will increase. If water continues to be available at depth it is probable that the DPD in the plant will not exceed 10 atm. (Renner, 1911; Nordhausen, 1917, 1921; Eaton, 1941; Stocking, 1945), and so absorption would appear to

cease when the TSMS in the surface horizons reached this value. Such a value would appear close to the permanent wilting percentage as determined in the laboratory.

If, on the other hand, only the surface horizons of soil are wetted and no supplementary source of water is available at depth, continued extraction can be expected from these horizons of fairly high root density until high TSMS values exist, as the DPD will increase proressively with the TSMS and the final TSMS which occurs will be limited more by the maximum DPD which the plant can withstand than by rate of supply of water. Measured DPDs in the conducting systems of trees under water stress have reached 200 atm. (MacDougal, 1926; Arcichovskij and Ossipov, 1931). In most herbs and shrubs it is probable that DPDs of 50-100 atm. could develop (Slatyer, 1957a).

From the literature the extent to which the soil water content can vary when moisture extraction appears to cease, is similar to that suggested above. Veihmeyer and Hendrickson (1927, 1928, 1934, 1948, 1949, 1955) and Hendrickson and Veihmeyer (1929 and 1945) found little evidence of water extraction, in field soils in which orchard trees were growing, below the permanent wilting percentage as obtained by a laboratory determination. Other workers, however, have shown that for field crops and orchard trees (Batchelor and Reed, 1923; Taylor and Furr, 1937; Cole and Matthews, 1939; Swezey, 1942; Haise, Haas and Jensen, 1955) and for natural vegetation (Alway, 1913; Burr, 1914; Alway, McDole and Trumbull, 1919; Taylor, Blaney and McLaughlin, 1934; Slatyer, 1957b) appreciable reductions of soil moisture occur below the permanent wilting percentage, extending sometimes significantly below the hygroscopic coefficient.

It would seem that the possible variation which can occur in the water extraction picture of any one soil horizon is too great to enable any general associations with the permanent wilting percentage, as determined in the laboratory, to be made, although for orchard trees under certain conditions it seems that reproducible values are obtained year after year (Veihmeyer and Hendrickson, 1950). This is supported on theoretical grounds as there seems no reason why transpiration and absorption should cease at any constant stress level. Laboratory experiments also support this contention, and for these reasons it would seem unwise to expect,

under a range of conditions, water extraction to cease at a value close to the permanent wilting percentage for any one soil.

Field determinations of the permanent wilting percentage are also frequently made by sampling when the plant appears wilted in early morning, although it is suggested that this provides an approximate value only (Hendrickson and Veihmeyer, 1929). Such a procedure depends for its reproducibility on the appearance of wilting being associated with a constant TSMS value of the soil mass.

Several factors influence the wilting behaviour of a field plant. The primary factors are those of root distribution and rate of water movement in unsaturated soils, as these determine whether or not sufficient water moves through the soil each night to eliminate TSMS gradients in the soil, so that the TSMS at the root surface is characteristic of that of the soil mass. Transpiration rate, by determining the extent of the water deficits developed each day by the plant and hence the amount of water required for absorption, can accentuate these factors. If severe water deficits develop on any day because of rapid transpiration, it is probable that if there is sparse root distribution and slow rates of water transport, not only would gradients in TSMS through the soil remain by sunrise, but also the total amount of water needed for absorption would not have been supplied. Thus a situation could arise in which there would be neither TSMS uniformity through the soil nor DPD-TSMS equilibrium between the plant and the soil at the root surfaces, and the appearance of wilting could result in a too high value being ascribed to the permanent wilting percentage. On the other hand, if the soil were actually dried to the permanent wilting percentage in the late morning, the appearance of wilting would be regarded as diurnal wilting only, and continued soil water depletion would occur until the determinations were made at sunrise the next day, resulting in a lower value than the correct one being obtained.

Even under constant and moderate rates of evaporation, errors could be introduced by the effect of slow rates of water movement and sparse root distribution causing the TSMS value at the root surface to be atypical for that of the soil mass. Cessation of root extension could accentuate these effects, and shrinkage of soil and root, so that there would be discontinuity in the soil-plant

system, could also delay attainment of DPD-TSMS equilibrium. Difficulties in reconition of wilting in xeric species could further influence the point at which DPD-TSMS equilibrium occurred.

The cumulative effects of these potential sources of error can be so great that Philip (1957) has estimated that the permanent wilting percentage, assessed on the basis of a permanently wilted appearance of the plant, can vary from close to field capacity to a value below that determined in the laboratory. As a result, application of this method to determinations of the permanent wilting percentage could probably result in extremely misleading results.

### Laboratory Determinations

The standard laboratory procedure for the determination of the permanent wilting percentage involves growing a plant in a small container under conditions of high water supply until its roots thoroughly explore the soil mass. The plant is then allowed to extract water from the soil without rewatering until an appearance of wilting is developed from which it will not recover in an approximately saturated atmosphere without further addition of water to the soil.

In laboratory determinations the sources of error due to lack of TSMS uniformity through the soil mass are reduced considerably because of the high root density which is developed. However, other possible sources of error exist from difficulties in the attainment of DPD-TSMS equilibrium at the point of zero turgor in the plant tissues, and because of variation in the DPD at zero turgor pressure.

The effect of most of the other factors mentioned in the previous chapter are of little influence to the attainment of DPD-TSMS equilibrium at the point of zero turgor pressure, as long as the experiment is conducted cautiously and sufficient time is allowed for possible recovery from wilting. Some idea of the extent of the errors associated with determinations on any one plant can be gained by an examination of the data available for sunflower, the plant most commonly utilised.

Richards and Weaver (1943) studied the soil moisture characteristics of soils on which permanent wilting percentage determinations had been made by Veihmeyer. They found that the soil moisture tension ranged from approximately 5-15 atm. at the

permanent wilting percentage, but, as the osmotic component of TSMS was not determined, the actual values of TSMS could not be estimated. Bodman and Day (1943), using freezing point determinations to measure TSMS directly, estimated that the TSMS at permanent wilting ranged from 10-22 atm., with a mean value of 18 atm. Their measurements were subject to some error in that the wilting symptoms were not normal (they observed wilting of upper leaves first) and they allowed only a few hours for recovery in the humid chamber. Thorne (1949) found very good agreement between 15-atm. soil moisture tension and permanent wilting percentage for a group of Hawaiian soils, in which, it is inferred, the osmotic concentration of the soil solution was low. Blair, Richards and Campbell (1950) utilised freezing point determinations to obtain a range of 10-22 atm. TSMS with a mean value of 18.5 atm. Richards, Campbell and Healton (1949) also utilised freezing point techniques and found a range of 7-35 atm., depending on the severity of the wilting symptoms at permanent wilting. Somewhat similar values were obtained by Richards and Weaver (1944) on soils which had been used for wilting determinations by Furr and Reeve (1945). Combining measurements of soil moisture tension and osmotic concentration of the soil solution, they found that at the first permanent wilting percentage, the TSMS for most of the 24 soils examined ranged from 7-16 atm., and at ultimate wilting, from 21-36 atm.

As determinations of TSMS are probably accurate only to within about 5 atm. (Richards, Campbell and Healton, 1949), the major source of variation in these experiments would appear to arise from the position of the leaf used as an indicator, and from the degree of wilting associated with permanent wilting by different observers. The possible extent of this variation, as indicated by the experiments of Furr and Reeve (1945) and Richards, Campbell and Healton (1949), would appear to be about 20 atm. for the sunflower plant.

Much of this error is avoided by adopting the Furr and Reeve concept of "first" and "ultimate" wilting, although with xeromorphic plants and other species with fairly rigid tissues, the appearance of wilting may not occur until DPDs much higher than those at zero turgor pressure exist (Briggs and Shantz, 1912a; Slatyer, 1957a).

The effect of size of container has been shown by Veihmeyer and Hendrickson (1934) to be of little significance and they also found little evidence of the influence of different evaporating conditions, as long as the determination was conducted when recovery had proceded to its limit in a humid chamber. This is supported by the general agreement noted above between investigations conducted at widely separated localities and is to be expected from theoretical considerations. For these reasons it is surprising that Caldwell (1913) and Shive and Livingston (1914) found a wide divergence in the permanent wilting percentage with different evaporating conditions. Such results are to be expected if the first evidence of diurnal wilting is used as an indicator (Brown, 1912), but these investigators took care to allow time for recovery in a humid chamber. In general, according to them, the observed value for the permanent wilting percentage increased progressively as evaporation increased, even under very low evaporating conditions. This is very difficult to explain, particularly in Shive and Livingston's (1914) study, since their experimental procedure was to place the plants in a humid chamber for 24 hours as soon as pronounced wilting was evident. The permanent wilting percentage should be unaffected by evaporating conditions, as long as sufficient time is available for recovery in the humid chamber, and as long as there is thorough root distribution in the pot. It is probably on this last feature that error may have entered their calculations, because in the treatment which contained the oldest plants at the commencement of the determinations, the differences in wilting coefficients found for different evaporating conditions was least. Also the degree of humidity may have been too low in the humid chamber for true DPD-TSMS equilibrium to be obtained, as it was observed that there was 0.1.-0.2 ml. of evaporation per hour from an atmometer in the chamber.

As long as determinations are conducted so that the plants are regularly watered in the developmental stage, the tendency for some species to develop high osmotic pressure is minimised, unless large quantities of solutes are present in the soil solution. This means that for most plants the DPD at zero turgor pressure—the point of permanent wilting—should probably not vary more than 30 atm., and the effect of this variation on the soil water content will be only one to two per cent, even in the finest textured soils.

Briggs and Shantz (1911a, 1911b, 1912a, 1912b, 1912c), in their extensive investigations, considered that the wilting coefficient was a soil constant unaffected by the type of plant used for the determinations. They conducted over 1300 determinations on 20 different soils; in general, the wilting coefficient for any one species varied by only about one per cent soil water content from the mean for all species. These results are somewhat surprising in view of the fact that their itemised data show that variation between some individual groups was up to 4.3 per cent soil water content on a soil for which the average wilting coefficient was 14.8 per cent. It is also surprising that the moisture equivalent/wilting coefficient ratio appeared so constant in these experiments as subsequent investigators (Veihmeyer and Hendrickson, 1928; Wadsworth, 1929; Shaw and Swezey, 1937; Duncan, 1939; Williams and Marshall, 1942) found that considerable variation existed in this relationship. In view of the importance of Briggs and Shantz's work, their results have been subject to little direct confirmation, and most studies which have supported the concept of a constant permanent wilting percentage for all plants have been conducted with common crop plants and mesophytes (Capulungan and Murphy, 1930; Hendrickson and Veihmeyer, 1929, 1945; Veihmeyer and Hendrickson, 1934, 1949). Briggs and Shantz's own experiments comprised about 1100 determinations with crop plants, of which 650 were with wheat, and only 16 determinations with xerophytes, 13 of which were made indirectly by using the wilting behaviour of wheat as an indicator.

This would suggest that, apart from experimental factors associated with the actual determinations of the permanent wilting percentage, the results of Briggs and Shantz and their supporters can be explained on the basis that the variation in the osmotic characteristics of the plants used was too small to cause significant differences in the soil water content at permanent wilting, even though the TSMS probably varied by up to 20 atm. from the mean value.

With woody plants and well developed native species, highly significant differences, even in soil moisture content, have been found to exist between plants at permanent wilting. Fowells and Kirk (1945) compared the permanent wilting percentage of year-old Ponderosa pine seedlings, transplanted into cans, with

sunflowers and found that on loam soil the moisture content at permanent wilting was 3-4 per cent lower with the pine seedlings. Lane and McComb (1948) measured ultimate permanent wilting percentages on well established plants of two tree species (green ash and black locust), brome grass and tomato. They found in a loam soil that the soil moisture contents for the different groups of plants were 7.7, 6.9, 5.9 and 10.2 per cent, respectively. No osmotic data were available from these tests, but it is evident that the TSMS, and hence the DPD, at permanent wilting in the native species was much higher than in the cultivated plants. Richards, Campbell and Healton (1949) found that the wilting range for cotton extended over the TSMS range of 12-43 atm., whereas the range for sunflowers was 7-35 atm. Moreover, in 14 of the 16 soils which they studied, the TSMS values were higher for cotton than for sunflowers. Wadleigh, Gauch and Strong (1947) observed that cotton could utilise more water from salinized soil than beans, corn or alfalfa. Slatyer (1957a) showed that the approximate first permanent wilting percentage for tomatoes grown under conditions of fluctuating water supply was at a TSMS of 27 atm., for Pima cotton 38 atm., and for year-old rooted privet cuttings it was 48 atm.

Part of the differences between the permanent wilting percentage for cultivated plants and those with more rigid tissues may be attributable to observer error in assessing wilting, but it is clear that the results still reflect marked differences in the osmotic characteristics of the various plants.

In general it may be stated that as long as a determination is conducted as suggested by Furr and Reeve (1945), experimental errors involved in laboratory determinations of the permanent wilting percentage are small and of insufficient extent to influence the value obtained. Climatic factors are likewise of slight importance, but the type of plant used can cause significant variation. In order to obtain reproducible values it would seem necessary that the determinations be conducted with commonly cultivated plants and mesophytes.

Two alternative laboratory methods for determining the permanent wilting percentage are worthy of mention. The first, which was intended for xerophytes, succulents and other species which do not readily exhibit wilting, was suggested by Briggs and Shantz

(1912a). It involved balancing the can containing the plant on a knife edge, each day, so that if more water was lost from the soil than from the plant, the soil end of the beam was elevated, or if more water was lost from the plant than from the soil, the soil end was depressed. Briggs and Shantz proposed that when the soil was moist, more water would be lost from the soil than from the plant, and that in systems drier than the permanent wilting percentage, the reverse would hold true. They suggested that the transition period represents the permanent wilting percentage, and found reasonable agreement with this stage and permanent wilting of other species. It is evident that errors could be introduced into these determinations as a result of the relative weights of plant and soil, and the TSMS/water content characteristics of the soil in relation to the DPD/water content characteristics of the plant. As soil water is removed most rapidly in the 0.1-1.0 atm. range of soil water tension, and depletion of plant water with increasing DPD is a more even process (Weatherley and Slatyer, 1957), it would seem that there would be a point at which the proportion of water lost from soil and plant would be reversed, but there would appear to be no valid reason why this should necessarily occur at the permanent wilting percentage. Since Briggs and Shantz themselves stated that the transition period is reflected in sluggish changes of the balance, the association they found could possibly have been due to inaccurate measurement. The fact that the method has remained virtually unused is evidence of its inherent weaknesses and lack of applicability.

The second method was described by Breazeale and McGeorge (1949) and was intended as a general determination of the permanent wilting percentage. It involves installation of a collar of soil around the stem of an actively growing tomato plant in the laboratory. Root penetration occurs into the collar, and the water content of the soil in the collar is presumed to be raised or lowered (depending on initial water content) to the permanent wilting percentage. The results obtained showed that the values were similar to those computed indirectly from the moisture equivalent. Although such an indirect estimation is itself liable to considerable error (Veihmeyer and Hendrickson, 1950), it could be expected that the TSMS in the collar would reach a value equivalent to the general DPD prevailing in the conducting system of the plant,

and hence of the probable order of 5-10 atm. (Renner, 1911; Nordhausen, 1917, 1921; Eaton, 1941; Stocking, 1945). The most significant feature of this method is that it would enable an approximate estimate of the permanent wilting percentage, as obtained with sunflowers, to be made. However, considerable variation in the value obtained could be expected, depending on the atmospheric conditions. If the determination were conducted in a humid chamber, the average DPD in the plant, and hence the TSMS in the soil collar, might not exceed two atm., and if the determination were conducted under very arid atmospheric conditions, the value may be 20-30 atm. Although in general the value may approximate the permanent wilting percentage obtained with other mesophytes, it has no essential relationship to the point of zero turgor in the plant under study or to other plants under different conditions, and would appear to be subject to errors of similar magnitude to those attached to the standard field determination.

## VII. SIGNIFICANCE OF THE PERMANENT WILTING PERCENTAGE AS A SOIL CHARACTERISTIC

For the permanent wilting percentage to be a significant value with respect to plant behaviour, it must not only be a soil water value at which all plants reach a stage of permanent wilting but must also mean something in terms of vital plant functions, such as elongation, growth or transpiration. Indeed it has always been assumed that it does mark a stage beyond which water is not available for normal plant functions, and the concept of "available" soil moisture has implied that the permanent wilting percentage represents the lower limit for normal vegetative growth of plants (Briggs and Shantz, 1912a, Veihmeyer and Hendrickson, 1950).

The discussion in Chapter IV provided evidence that the effects of water stress on plant response are caused in the first instance by a development of water deficits in the plant systems which have direct and indirect effects on elongation, vegetative growth and transpiration. It was also deduced that these functions are not necessarily affected in the same manner or to the same extent by a similar degree of stress and that different plants and different tissues also respond differently. In general, although the effects of

stress are usually apparent at low TSMS values, it appears that most active processes cease either before or at the DPD which exists at zero turgor pressure. This value varies from tissue to tissue within any one plant, so that, although it may be recognizable for leaf tissue by the wilted appearance of the leaves, its interpretation as a point representing cessation of the functions of the whole plant must be undertaken with caution, particularly since some processes—for instance, cell enlargement—may be completely inhibited at lower tensions. However, it can be appreciated that when a DPD exists such that there is zero turgor pressure in the active leaves, most processes associated with plant growth will have ceased.

This suggests that the permanent wilting percentage, associated as it is with the condition of zero turgor pressure in the leaves, represents a point for any one plant beyond which most physiological processes would not be expected to proceed, rather than a soil value applicable to all plants and at which plant functions cease.

The question which then arises concerns the constancy of the permanent wilting percentage as a soil value. If the variations in osmotic pressure, and hence in TSMS, at permanent wilting are not extreme, the variations in soil water content—the method of expression of the permanent wilting percentage—may be small enough to be ignored. On the other hand, if wide variations in soil water content can be expected, the significance of the permanent wilting percentage as a universal index for all plants is considerably reduced. In order to evaluate this point it is necessary to determine what significance the observed values of the permanent wilting percentage have, in relation to the methods used in their determination.

The significance of field determinations of the permanent wilting percentage, based on the cessation of water extraction from any one soil horizon, is reduced not only by the errors inherent in the determination but also by the fact that the actual stage at which the determination is made is not necessarily related to the permanent wilting of the plant.

Transpiration, which is the ultimate factor determining cessation of water extraction, is primarily a passive process, not controlled directly by turgor levels, and so does not necessarily cease at any

particular stress level. For reasons given previously, the degree of reduction of transpiration with increasing TSMS varies considerably from plant to plant, and absorption of soil water may not cease, even after death, until there is vapour pressure equilibrium between atmosphere and soil. It was suggested that in plants such as orchard trees, with access to water at depth in the soil, soil water extraction in the surface few feet of soil may appear to cease at a TSMS value close to that obtained for permanent wilting of sunflowers in containers. This is by no means an essential relationship, however, many plants exhibiting different soil water extraction patterns, and the fact that cessation of extraction is not necessarily related to the permanent wilting of the plant in question (Hendrickson and Veihmeyer, 1945) demonstrates that the determinations have little real application to wilting phenomena.

For these reasons it would seem that the standard field method for measuring the permanent wilting percentage provides results which not only vary too much in different plant-soil systems to provide values which could be regarded as soil constants, but which also, in any one plant-soil system, do not necessarily reflect the TSMS at permanent wilting. From both these respects, therefore, the method has little significance when interpreted over the whole range of plant species.

Determination of the permanent wilting percentage by utilising, as an indicator, the morning wilt of plants growing in the field, is also subject to considerable error as it cannot be determined whether or not the wilted appearance is due to true DPD-TSMS equilibrium or to a lag of absorption behind transpiration. It is unfortunate that measurement difficulties invalidate this type of field determination, for it has the great advantage over other methods that it attempts to interpret the wilting behaviour of a plant in its natural habitat. The determinations, therefore, have more potential significance than those made by the standard field or laboratory determinations.

As distinct from the field methods of determining the permanent wilting percentage, the laboratory method, if conducted with due regard for the precautions observed by Furr and Reeve (1945), is subject to few serious sources of error, particularly if determinations are made on common crop plants or mesophytes, and re-

producible values can be obtained for different plants on the same soil (Briggs and Shantz, 1912a; Veihmeyer, 1956), or for the same plant on a range of soils if the values are interpreted on the basis of TSMS (Richards and Weaver, 1944).

It was suggested above that the main reason for this apparent constancy of the permanent wilting percentage as a soil value, particularly when expressed as soil water content, is that when plants from sub-humid and arid habitats are grown under conditions of high water supply and absence of water stress, the anatomical structure and osmotic pressure characteristic of the plants in their natural habitat do not develop to the same extent and the DPD at which permanent wilting occurs is reduced to a level more characteristic of mesophytes. As a result the TSMS at permanent wilting, which in nature may have a potential range of 5-200 atm., in the laboratory may not exceed 30 atm. for most plants, an order of variation which would be represented by not more than about two per cent soil moisture content, even in the finest textured soils.

This means that the permanent wilting percentage, as determined under standard laboratory conditions and interpreted in terms of soil water content, is an approximate soil constant, but that the degree of constancy is misleading, depending, as it does, on growing plants from widely different habitats in a uniform, mesic environment, so that the potential variation between species does not develop.

Therefore, determinations of the permanent wilting percentage, instead of having universal application, can be applied strictly only to conditions which do not differ significantly from those of the determination itself. This limitation is at once evident when, to envisage an extreme case, the permanent wilting percentage of a halophyte might be determined in the laboratory as 30 atm., whereas the same species might be found growing and non-wilted at a TSMS of over 100 atm. in its natural habitat.

Although this criticism appears to be well founded, the concept of the permanent wilting percentage as a soil constant must still be considered to have value as a general guide to the lower limit of soil water availability if the variation in osmotic pressure found in practice in most plants does not significantly affect the soil water content at permanent wilting.

For most cultivated plants the osmotic pressure lies within the approximate range of 10-20 atm. (Iljin, 1927; Magistad, 1945; Stocking, 1956). Few mesophytes have values beyond 30 atm., although aquatic plants may have values below five atm. (Maximov, 1929). Xerophytes in general have values of from 20-50 atm., halophytes up to 100 atm. with extreme cases of twice this value, depending largely on seasonal conditions (Maximov, 1929; Walter, 1931; Harris, 1934). This indicates that for most plants of humid environments, and for most cultivated plants, the permanent wilting percentage, as determined on a laboratory basis, which approximates 10-20 atm. and has a mean value of about 15 atm. (Thomas, 1921; Edlefsen, 1934; Schofield and da Costa, 1935; Bouyoucos, 1936; Bodman and Day, 1943; Anderson and Edlefsen, 1942; Richards and Weaver, 1943, 1944; Robertson and Kohnke, 1946; Richards, Campbell and Healton, 1949; Veihmeyer and Hendrickson, 1949), could provide an estimate within two per cent soil water content of the true value, and frequently within one per cent. For xerophytes and halophytes growing in their natural environments, however, the laboratory determinations could be in error to the extent of four per cent or more, and the results would have no valid application.

On this basis it seems that the permanent wilting percentage, as determined in the laboratory, can provide a general index to the lower limit of available water for most cultivated plants. However, it is doubtful that it is wise, or strictly valid, to adopt a value which applies only because the variation in osmotic pressure between most crop plants does not significantly affect the soil water content at permanent wilting. Certainly in critical studies, dealing with TSMS instead of soil water content, adoption of such an index could be quite misleading, and it is probably for this reason that many studies which have attempted to relate the responses of a particular plant to the permanent wilting percentage, as determined with sunflowers or as estimated from the 15-atm. soil water retention value, have failed to provide the expected results.

Literal application of permanent wilting percentage data to field conditions have likewise to be undertaken with caution, as the factors which can invalidate the field methods of measurement of the permanent wilting percentage by causing lack of uniform-

ity of TSMS in the soil mass and lack of attainment of DPD-TSMS equilibrium, also influence the availability of soil water to plants, regardless of the TSMS at true permanent wilting. Thus any application of permanent wilting percentage data to field conditions can really be interpreted only in terms of the morphological and physiological characteristics of the plant (and the adjacent plants) in the field, of the water transmission and retention characteristics of the soils, and of the climatic conditions.

The true significance of the permanent wilting percentage in studies of plant and soil water relationships is clarified by examining the data with respect to the purpose to which any particular study is to be directed. If all that is required is a general guide to the lower limit of available water for crop plants, it seems that such a guide is indeed provided by the standard laboratory determinations. If, on the other hand, a more critical application is desired, it must be realised that all that is achieved by a laboratory determination is an approximate indication of the 15-atm. TSMS value. The most that can be achieved by a field determination is an approximate estimation of the laboratory value. Admittedly, if laboratory determinations are conducted with only one plant, as is already the tendency with sunflowers, and the procedure is standardised as much as possible, the accuracy of estimation is such that variation may not exceed 10 atm. TSMS, but still nothing more is achieved than such a standardisation of a plant-soil system that the plant is of no consequence, and the only significance attached to the determination is that it is a reasonable estimate of a physical soil characteristic.

For these reasons there would seem to be a strong case for the elimination of direct determinations of the permanent wilting percentage altogether, and their replacement with physical determinations of the TSMS at, say, 15-atm. level. Such determinations would have the advantage of reproducibility and accuracy, would not have the misleading associations with wilting phenomena, and would have equal applicability as a general guide to the lower limit of available soil water for crop plants. Similar determinations, at other TSMS levels, could possibly be used as guides to lower limits of available water for other ecological groups of plants, but because of the limited applicability attached to any general values and the difficulty of interpretation of such values under natural

conditions, it is doubtful that they would have any worthwhile significance.

For critical ecological and physiological studies, involving responses of plants to specific TSMS and DPD values, general values such as those from laboratory determinations or from physical determinations at 15-atm. TSMS are of little significance. Permanent wilting as a plant phenomenon, with its close relationship to the point of growth cessation, is clearly of considerable importance; the permanent wilting percentage, representing the soil water content at the point of permanent wilting, is likewise of significance to any one plant under known conditions. However, the TSMS at this value will vary from species to species and within any one species, depending on the environmental conditions and the preconditioning of the plant. As a result, application of data from any one plant, obtained under certain conditions, to any other plant under different conditions, can be conducted only when the order of variation introduced, particularly with respect to the physiological status of the plant and to its root distribution in the soil, does not vary significantly between the two situations.

## VIII. GENERAL SUMMARY

Ever since the comprehensive studies of Briggs and Shantz, the permanent wilting percentage, expressed in terms of soil water content, has been regarded as a highly significant soil water value, indicating the lower limit of available soil water for plant growth on any one soil, and as unaffected by atmospheric conditions or the plant under study. Because a plant does not respond in terms of soil water content but in terms of total soil moisture stress (TSMS), the permanent wilting percentage has also been regarded not only as a constant for any one soil but as occurring at an approximately constant TSMS in all soils.

The present discussion has brought forward the thesis that, instead of being a soil constant, the permanent wilting percentage is essentially dependent upon the plant under study, as the osmotic pressure of the plant leaves is fundamentally the factor determining the point at which permanent wilting occurs.

The argument is advanced that as a plant depletes the soil water reservoir, the TSMS increases, and the diffusion pressure deficit (DPD) in the plant must also increase, because recovery in turgor

each night cannot continue after there is DPD-TSMS equilibrium. This progressive onset of stress continues until the TSMS reaches a level equivalent to that of the osmotic pressure in the plant leaves, at which point there can be no recovery of turgor by the leaves, for DPD-TSMS equilibrium is at a DPD such that there is zero turgor pressure. At this point most active plant processes would be expected to cease, and the leaves to be permanently wilted if their structural characteristics permit the appearance of wilting. It is proposed that this is the fundamental point at which the permanent wilting percentage occurs and as such is theoretically controlled, not by any soil characteristics but by the osmotic characteristics of the plant.

In practice, the factors which affect the attainment of DPD-TSMS equilibrium at zero turgor pressure, and hence affect the determination of the permanent wilting percentage, vary according to the manner in which a determination is conducted. In the standard laboratory technique the sources of error are small, and reproducable values are obtainable for most plants as long as they are grown under standard conditions. Field determinations of the permanent wilting percentage are, on the other hand, subject to errors of considerable magnitude, whether the apparent cessation of water extraction from any one soil horizon is used as an indicator, or whether the determination is made on the basis of a wilted appearance in early morning.

Apart from the factors which affect the reproducibility of determinations, others operate to limit the significance of the values obtained for the permanent wilting percentage. The primary factor is that the standard laboratory procedure for determining the permanent wilting percentage serves to adjust the osmotic characteristics of the plants examined to those more typical of plants growing in humid environments, such as mesophytes. This means that the permanent wilting percentage is usually determined within a TSMS range of 5-30 atm., with a mean value of about 15 atm., and so appears to be an approximate soil constant when interpreted on the basis of soil water content. Theoretically, however, the variation in TSMS at permanent wilting parallels the variation in the osmotic characteristics of different plant species in different habitats and so has a potential range of 5-200 atm. Therefore any standard value attributed to the permanent wilting percentage,

and hence attributed to the osmotic characteristics of the plant, fails to take account of this potential variation and its practical significance.

The true significance of permanent wilting in any one plant-soil system is the close association it has with growth cessation. Because of the importance of this association, the soil water content at permanent wilting, which is the permanent wilting percentage, is likewise of considerable significance in any one system as the lower limit of soil water available for plant growth. For critical studies in plant-soil water relationships, generalisation beyond this point results in the introduction of error, so that the results of a permanent wilting percentage determination can strictly be applied only to the system from which they are obtained. For general purposes, however, such accuracy is not necessary, and because groups of plants with similar osmotic characteristics wilt at similar TSMS values, it is possible to associate a single value for the permanent wilting percentage with wilting phenomena of the plants within any one group. Thus the standard laboratory determination, which in effect estimates a range of osmotic pressures characteristic of most crop plants and mesophytes, can be used to provide a general index of the lower limit of soil water availability for growth of these species.

This, however, appears to be the limit to which data from standard determinations can be applied, as their application to other groups of plants with different charactersitics, such as species from saline or arid habitats, would have no relationship to the wilting phenomena of these species and would be quite misleading as an index of growth cessation.

Therefore, instead of having universal application to all species, the permanent wilting percentage has limited application and is of significance only to restricted groups of plants. Because of the conditions under which they are conducted, all that laboratory determinations really provide is an approximate estimation of a TSMS value at about 15-atm. level. Because of the experimental errors inherent in their measurement all that the field determinations really provide is an approximate estimation of the laboratory value. For these reasons it is suggested that if there truly is a need for an approximate and general reference point for soil water availability, a case exists for the elimination of direct determina-

tions of the permanent wilting percentage and their substitution with physical soil determinations at TSMS levels of, say, 15 atm. Such determinations would have the advantage of increased precision and reproducibility, they would not have the implicit but misleading association with wilting phenomena, and they could be regarded as providing an approximate indication of the lower limit of soil water available for growth of crop plants. They could also perhaps be applied as approximate indicators for other ecological groups of plants if the TSMS levels were adjusted to those appropriate to the range of osmotic pressures encountered in the species to be studied.

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